Effects of ALS-inhibitor herbicides, crop sequence, and fertilization on natural soil suppressiveness to *Striga hermonthica*

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Abstract

Striga hermonthica remains one of the greatest biological threats to cereal production in the savannahs of sub-Saharan Africa. Control efforts at the International Institute of Tropical Agriculture (IITA), Nigeria, focus on developing integrated *S. hermonthica* management (ISM) options such as legume-cereal rotation, use of host–plant resistance, soil-based biological control exploiting enhancement of naturally occurring biotic soil suppressiveness, and use of acetolactate synthase (ALS)-inhibiting herbicides as host–crop seed treatments. We investigated, in pots, if soybean crops with or without fertilizer (N, P, or NPK) and preceding a maize crop used as a bioassay enhanced biotic soil suppressiveness to *S. hermonthica,* and if the ALS-inhibitor herbicides, imazaquin and nicosulfuron, used to control weeds in preceding crops constitute any risk to this biotic system. Factors tested included: (1) crop preceding bioassay maize (soybean [EMGOPA] versuss maize [8338-1]); (2) herbicide weed control in preceding crop (imazaquin in soybean and nicosulfuron in maize versus hand weeding); (3) fertilizer application to preceding crop ($90 \, kg \, N \, ha^{-1}$, $40 \, kg \, P \, ha^{-1}$; $90 \, kg \, NPK$; versus no fertilizer); (4) soil treatment before planting bioassay maize (pasteurized soil versus non-pasteurized soil). Effects of treatments on biotic suppressiveness were evaluated by comparing effects of treatments in non-pasteurized soil with those of the same treatments in pasteurized soil. Results indicated that biotic soil suppressiveness to *S. hermonthica* existed naturally in the soil used and was enhanced by a preceding soybean crop and application of N, P or NPK fertilizers. Weed control using ALS-inhibiting herbicides in the preceding crops, particularly imazaquin applied in soybean, had a negative effect on natural soil suppressiveness to *S. hermonthica* parasitism in maize. Results of this study further confirm the biotic nature of soil suppressiveness to *S. hermonthica*, and stress its important role in ISM. Land-based management strategies for *S. hermonthica* control, such as legume crops in rotation to enhance soil N and fertilizer application appear to directly enhance soil suppressiveness to *S. hermonthica*.

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Because ALS-inhibiting herbicides pose a risk to biotic soil suppressiveness, their use as a primary control measure for *S. hermonthica* control in Africa may not be a sustainable approach.

1. Introduction

Striga hermonthica (Del.) Benth. is an obligate root–parasite that is indigenous to Africa and causes severe losses in most cultivated cereal crops in the continent. Incidence and severity of *S. hermonthica* infection is particularly high in the savannas of West Africa on sorghum (*Sorghum bicolor* L.), pearl millet (*Pennisetum glaucum* (L.) R. Br.) and maize (*Zea mays* L.) with an estimated annual yield loss of US$ 7 billion, resulting in adverse effects on the lives of over 100 million African people in the savannah regions of West Africa (M'boob, 1989).

Intensification of land use, reflected in intensive cereal mono-cropping with little or no fallow or rotation to non-host crops, has contributed to increased *Striga* spp. problems in Africa (Berner et al., 1996). This has occurred as a result of unintentional contamination of fields with *Striga* spp. seeds, and the continual cultivation of susceptible crops that leads to the production of more *Striga* seeds (ca. 500,000 per plant) (Bebawi et al., 1984; Berner et al., 1994a). As intensification of land use increases, field contamination and parasite reproduction also inexorably spread.

A major constraint to effective control of *S. hermonthica* is that it causes up to 75% of its overall damage to the host during its subterranean stage, emerging usually after the last weeding has taken place (Parker and Riches, 1993). Consequently, control targeted at only emerged *S. hermonthica* plants frequently does not result in increased crop yield. Recent efforts at the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria, focus on developing integrated *S. hermonthica* management options such as legume rotation, use of host–plant resistance, soil-based biological control and use of acetolactate synthase (ALS)-inhibiting herbicides as host–crop seed treatments (Berner et al., 1994b, 1995, 1996, 1997a). Use of legumes as trap crops to reduce the *Striga* seed bank in a cereal-legume rotation is a core strategy to which other options can be added. Farmers using this integrated strategy in Africa have dramatically increased their food production and on-farm income (Berner et al., 1995; Carsky et al., 2000; Oswald and Ransom, 2001; Gbèhounou and Adango, 2003; Schulz et al., 2003).

Soils that are suppressive to *Striga* spp. are widespread in Africa (Odhiambo and Ransom, 1994; Berner et al., 1996; Gbèhounou et al., 1996). Odhiambo and Ransom (1994) found that the rate of *S. hermonthica* seed bank demise in suppressive soils was much greater than could be achieved by any other management practice including the use of trap crops and hand weeding. Berner et al. (1996), Pieterse et al. (1996) and Ahonsi et al. (2002a,b) demonstrated that natural soil suppressiveness to *S. hermonthica* is of microbial origin, leading to the question of how to manage soils and crops to maximize suppressiveness to *S. hermonthica.* Berner et al. (1996) investigated soil samples from 14 different locations in Nigeria and found that about half of these across the country were naturally suppressive to *S. hermonthca* (only if the soil was not steam pasteurized). They concluded that natural soil suppressiveness to *S. hermonthica* is widespread in West Africa and that the phenomenon is biotic (likely microbial) in nature since it can be eliminated by soil steaming. Ahonsi et al. (2002a) further demonstrated this biotic nature of soil suppressiveness to *S. hermonthica* and suggested that the existence or non-existence of this phenomenon may partly explain the wide variation of effects of nitrogen fertilizers on *S. hermonthica* parasitism usually observed in different soils and experiments by many researchers. Ahonsi et al. (2002b) isolated from different suppressive soils from Abuja, Bida, Mokwa, and Ibadan locations in Nigeria, rhizosphere fluorescent pseudomonads that inhibited germination of seeds of *S. hermonthica* and restored soil suppressiveness to the parasite in soils where suppressiveness was eliminated by steaming.

A very important aspect of enhancement of naturally suppressive conditions is nitrogen fertility

(Berner et al., 1996; Ahonsi et al., 2002a), which may be addressed through legume rotation, and supplemental inorganic fertilizers. On the other hand, it is important to evaluate the potential risk of synthetic pesticide-based technologies on naturally occurring soil suppressiveness to *S. hermonthica*, particularly, use of acetolactate synthase inhibiting herbicides in the control of *Striga* spp. (Abayo et al., 1996, 1998; Berner et al., 1994b, 1995, 1996, 1997a; Kanampiu et al., 2003). Chemical herbicides when translocated to the root systems or applied pre-emergence to the soil directly or by seed dressing, could have a detrimental effect on soil biota (Bollen, 1961; Levesque and Rahe, 1992) and, consequently on biotic soil suppressiveness. ALS-inhibiting herbicides are those that kill weeds by inhibiting the enzyme, ALS, also called acetohydroxyacid synthase (AHAS), which catalyzes the synthesis of the branch-chain amino acids (valine, leucine, and isoleucine) in plants and microorganisms (Whitcomb, 1999; Potera et al., 2002). They include four classes of herbicides: sulfonylureas, imidazolinones, triazolopyrimidines, and pyrimidinyl thiobenzoates. Release of these herbicides into the soil to control *S. hermonthica* may negatively influence microbial soil suppressiveness (Potera et al., 2002), and other soil-based *S. hermonthica* management systems such as crop rotation and fertilizer application which are dependent on this biotic system (Ahonsi et al., 2002a). In this study, we investigated if soybean crops with or without fertilizer (N, P, or NPK), preceding a maize crop used as a bioassay, enhance biotic soil suppressiveness to *S. hermonthica*, and if the use of imazaquin and nicosulfuron, both ALS-inhibiting herbicides, to control weeds and *S. hermonthica* in a preceding crop pose any risk to biotic soil suppressiveness to *S. hermonthica* in maize.

2. Materials and methods

Pot experiments were carried out in a screenhouse (screens off direct rain water, insects and rodents) at IITA, Ibadan, Nigeria under alternating day light and night darkness, and ambient temperature (23–30 °C) and relative humidity.

Seeds of *S. hermonthica* used for this study were collected from *S. hermonthica* plants growing on sorghum (*S. bicolor* L.) fields at Bida, Nigeria

(9°05′N and 6°01′E) 6–12 months prior to the experiments. The seeds were stored at ambient temperature (26–33 °C) in polyethylene containers in a laboratory at IITA, Ibadan, Nigeria. Approximately 3000 germinable *S. hermonthica* seeds (Berner et al., 1997b) were used per infested pot (156.25 cm^2 surface area and 4 kg soil). Infestation of soil with *S. hermonthica* seeds was carried out by thoroughly mixing the top 5 cm layer of soil in the pot with the seeds in a plastic tray. The soil–parasite seed mixture was then returned to the pot, and watered.

Soybean seeds (var. EMGOPA) were obtained from the Grain Legume Improvement Program of IITA, and seeds of a maize hybrid, 8338-1, susceptible to *S. hermonthica* were obtained from the Maize Improvement Program of IITA, and used in this study.

Compound NPK (15:15:15), urea (46% N) and single super-phosphate (SSP) (18% P$_2$O$_5$) were used in the study. All the fertilizers were obtained from the Nigerian Fertilizer Company, Port-Harcourt, Nigeria through the IITA Fertilizer Procurement unit. The amount of fertilizer needed per pot in each treatment was calculated using the standard hectare furrow slice method.

The ALS-herbicides used in this study were an imidazolinone, imazaquin (Scepter®, (*RS*)-2-(4-iso-propyl-4-methyl-5-oxo-2-imidazolin-2-yl) quinoline-3-carboxylic acid) (Anonymous, 1996a) and a sulfonylurea, nicosulfuron (Accent®, 2-(4,6-dimethoxypyrimidin-2-ylcarbamoylsulfamoyl)-*N,N*-dimethylnicotinamide) (Anonymous, 1996b).

Soils obtained from farm land in a location in Ibadan (7°17′N, 3°30′E), Nigeria previously identified to be highly suppressive to *S. hermonthica* (over 55% reduction in *S. hermonthica* compared with pasteurized soil) (Berner et al., 1996; Ahonsi et al., 2002a) were used. Non-suppressive soils used as checks, were obtained by pasteurizing the suppressive soils in plastic pots (18 cm diameter, 17.5 cm depth, perforated at the bottom) in a steaming machine as described in Ahonsi et al. (2002a).

Since this was a crop rotation study, two stages of cropping were involved. A total of 32 treatment combinations arranged in $2^3 \times 4$ factorial were tested in a randomized complete block design (RCBD), replicated eight times and the experiment was repeated. Factors tested included: (1) preceding crop at two levels (soybean-maize versus maize-maize); (2) weed

control at two levels (herbicide versus hand weeding); (3) fertilizer application at four levels (90 kg N ha^{-1}, 40 kg P ha^{-1}; 90 kg NPK; and no fertilizer); (4) soil at two levels (natural non-pasteurized soil (suppressive soil) versus pasteurized soil (non-suppressive soil)).

In the first cropping cycle, 256 pots (156.25 cm^2 surface area) were filled with soil. One half the total number of pots was infested with *S. hermonthica* seeds at 3000 germinable seeds per pot (Berner et al., 1997b), leaving the other half non-infested. The pots were kept moist for 2 weeks to condition the *S. hermonthica* seeds for germination (Worsham, 1987) before planting. One half of the pots were planted to soybean variety, EMGOPA, and the other half to maize hybrid, 8338-1. Six soybean seeds or three maize seeds were sown per pot; later the seedlings were thinned to two plants and one plant, respectively. Imazaquin at a total concentration of 134 g a.i. ha^{-1} (656 μg a.i. per pot) was applied to soybean, and nicosulfuron at 47 g a.i. ha^{-1} (230 μg a.i. per pot) was applied to maize. Each herbicide was applied in two splits (pre-planting (5–6 h before planting) and post-planting (3 weeks after planting)). The controls were hand-weeded soybean or maize (no herbicide).

Application of herbicide was done by dissolving herbicide in water and spraying soil from a spray bottle, calibrated to deliver the volume equivalent to the required dose at a fixed number of sprays. Fertilizer application was by top dressing, at 1 week after planting. Fertilizer application rates were 0.36 g urea per pot (≡90 kg N ha^{-1}), 0.89 g SSP per pot (≡40 kg P ha^{-1}), and 1.07 g NPK (15:15:15) per pot (≡90 kg balanced NPK ha^{-1}). The N and NPK, and P fertilizer regimes tested in pots are around the same regimes mostly used by farmers in the region for cereals and legumes, respectively. The control treatment was not fertilized. Number of emerged *S. hermonthica* plants was observed and recorded from the maize pots weekly from time of first parasite emergence until 12 weeks after planting (WAP). All the maize plants were harvested 12 WAP and aboveground dry-weight taken.

To bioassay the effects of the various treatments applied at the first cropping cycle, all the pots previously infested with *S. hermonthica* seeds were pasteurized and the non-infested pots were left non-pasteurized (natural soil) before the second cropping cycle. All the pots were then infested with *S. hermonthica* seeds and conditioned for 2 weeks before they were planted

to maize hybrid, 8338-1. One maize plant was maintained per pot, and 15 kg NPK ha^{-1} equivalent was applied to all the pots at one WAP. Number of emerged *S. hermonthica* was counted and recorded from the time of first parasite emergence until 12 WAP. The maize shoots, harvested at 12 WAP by cutting just above the soil level, were oven-dried for 72 h at 80 °C after which the weights were taken using a balance (Mettler PM4000). The experiment was repeated.

Since variances from repeated experiments were homogeneous, data (greatest number of emerged *S. hermonthica* per pot from the weekly counts, and maize shoot dry-weight per pot at harvest) from repeated experiments were pooled. These were subjected to analysis of variance (ANOVA) using the MIXED procedure in SAS (Littell et al., 1996). Replications were treated as random, and treatments as fixed effects. Single-degree-of-freedom contrasts were made to test differences between specific treatment means. Number of emerged *S. hermonthica* were square-root transformed and used for statistical analysis to determine levels of significance associated with differences in means.

3. Results

In the first cropping cycle of the rotation trial, applying nicosulfuron to maize resulted in over 80% reduction ($P < 0.001$) in the number of emerged *S. hermonthica* and a concomitant significant increase in aboveground maize biomass compared with the hand weeded treatment (Table 1). Independent of herbicides application (i.e. in hand weeded treatments), fertilizer (equivalent to 90 kg N ha^{-1}) application to maize also reduced ($P < 0.001$) the number of emerged *S. hermonthica* by over 80%, and increased ($P < 0.05$) maize biomass by over 45% compared with no fertilizer application (Table 1). Similarly, application of NPK (15:15:15) (at 90 kg ha^{-1}) resulted in significant reduction in the number of emerged *S hermonthica* ($P < 0.01$) with an increase also in maize biomass (Table 1). Application of P fertilizer (equivalent 40 kg P ha^{-1}) did not result in significant effects on *S. hermonthica* parasitism in maize (Table 1).

Results of the second cropping cycle bioassay (Tables 2–4) indicated a significant reduction in the number of emerged *S. hermonthica* plants and a

Table 1

Effects of the ALS-inhibiting herbicide nicosulfuron and N, P, NPK fertilizer application to the current maize crop on number of emerged *Striga hermonthica* in maize hybrid, 8338-1 and aboveground maize biomass

Treatment	*S. hermonthica* count per pot			Maize biomass (g per pot)		
	Mean	±S.E.	$P > F$	Mean	±S.E.	$P > F$
Herbicide						
Nicosulfuron (*a*)	1.1	0.75	<0.001	28.9	1.26	<0.001
No herbicide (*b*)	6.5			20.2		
Fertilizer						
No fertilizer	6.6			19.4		
90 kg N ha^{-1}	2.1	1.14	0.07	30.5	1.65	<0.001
40 kg P ha^{-1}	3.7			20.7		
90 kg NPK ha^{-1}	2.8			27.5		
Herbicide + fertilizer						
No herbicide + no fertilizer (*c*)	11.1			16.7		
Nicosulfuron + no fertilizer	2.1			22.0		
Nicosulfuron + 90 kg N ha^{-1}	2.1			36.2		
Nicosulfuron + 40 kg P ha^{-1}	0.0	1.50	0.02	24.5	2.23	0.53
Nicosulfuron + 90 kg NPK ha^{-1}	0.1			32.8		
No herbicide + 90 kg N ha^{-1} (*d*)	2.1			24.8		
No herbicide + 40 kg P ha^{-1} (*e*)	7.4			16.8		
No herbicide + 90 kg NPK ha^{-1} (*f*)	5.4			22.3		
Specific contrasts	Estimated difference (%)					
b − *a*	−82.0***			31.5*		
d − *c*	−80.9***			48.2*		
e − *c*	−33.7			0.4		
f − *c*	−51.7**			32.9		

±S.E.: standard error of mean.
* Significant at 5% probability.
** Significant at 1% probability.
*** Significant at 0.1% probability.

significant increase in aboveground maize biomass in natural soil compared with pasteurized soil. Similarly, where soybean was the preceding crop, there was a significant ($P = 0.05$) reduction in the number of emerged *S. hermonthica* in a subsequent maize crop and a significant increase in aboveground maize biomass (> 50%) compared with the maize-maize crop sequence (Table 2). Herbicide application particularly to a preceding soybean crop interacted significantly with crop sequence and fertilizer application in natural soil, but not in the pasteurized soil (Tables 3 and 4). In natural soils that received no herbicide application, the preceding soybean crop significantly ($P \leq 0.001$) reduced the number of emerged *S. hermonthica* by > 40% and increased ($P \leq 0.001$) the aboveground biomass of the subsequent maize crop by >150% compared with maize grown after a maize crop receiving no herbicides (Table 3). However, in pasteurized soil, only the biomass of maize grown after a soybean crop increased significantly ($P \leq 0.001$) compared with maize grown after a maize crop (Table 3).

The number of emerged *S. hermonthica* in maize grown in natural soil that had herbicide application in the immediate preceding crop was higher ($P \leq 0.001$) than that without herbicide. Furthermore, there was over a 40% reduction in biomass of maize grown in natural soils that had herbicide application in the preceding crop compared with maize grown in natural soils that had no herbicide application. Specifically, in natural soil, number of emerged *S. hermonthica* in maize grown after a soybean crop that received an imazaquin application was 60% higher ($P \leq 0.001$)

Table 2
Effects of soil pasteurization, preceding crop, herbicide, and N, P and NPK fertilizer application to preceding crop of soybean or maize on the number of emerged *Striga hermonthica* plants in maize (8338-1) and aboveground maize biomass

Treatment effect	Number of emerged *S. hermonthica* per pot		Aboveground maize biomass (g per pot)	
	Overall mean	LSD	Overall mean	LSD
Soil pasteurization				
Pasteurized soil	23.5	1.48	6.3	0.68
Natural soil	19.4		9.1	
Preceding crop				
Maize	22.2	1.48	4.2	0.68
Soybean	20.7		11.3	
Application of herbicide to preceding crop				
Herbicide	22.0	1.48	6.8	0.68
No herbicide	20.9		8.6	
Application of fertilizer to preceding crop				
No fertilizer	21.3		5.3	
90 kg N ha^{-1}	21.7	2.01	9.1	0.99
40 kg P ha^{-1}	21.3		8.3	
90 kg NPK ha^{-1}	21.5		8.2	
Interactions				
Crop × soil	***		NS	
Crop × herbicide	**		NS	
Soil × herbicide	***		NS	
Crop × soil × herbicide	**		NS	
Soil × fertilizer	*		NS	
Crop × soil × fertilizer	NS		*	

NS: not significant.
* Significant at 5% probability.
** Significant at 1% probability.
*** Significant at 0.1% probability.

Table 3
Effect of applying the ALS-inhibiting herbicides imazaquin to a preceding soybean crop and nicosulfuron to a preceding maize crop on the number of emerged *Striga hermonthica* plants in maize and aboveground biomass of maize in natural and pasteurized soil

Treatment	Natural soil		Difference	Pasteurized soil		Difference
	Herbicide	No herbicide		Herbicide	No herbicide	
Emerged *S. hermonthica* per pot						
Maize	21.4	22.0	−0.6	21.8	23.4	−1.6
Soybean	21.0	13.1	7.9***	23.7	25.2	−1.5
Difference	0.4	8.9***		−1.9	−1.8	
Aboveground maize biomass (g per pot)						
Maize	3.4	6.0	−2.6***	3.4	3.9	−0.5
Soybean	11.4	15.7	−4.3**	9.2	8.9	0.3
Difference	−8.0***	−9.7***		−5.8***	−5.0***	

** Significant at 1% probability.
*** Significant at 0.1% probability.

Table 4
Effect of N, P, and NPK fertilizer application to a preceding soybean or maize crop without herbicide application on the number of emerged *Striga hermonthica* plants in maize and aboveground biomass of maize in natural and pasteurized soil

Treatment	Natural soil		Difference	Pasteurized soil		Difference
	Maize	Soybean		Maize	Soybean	
Emerged *S. hermonthica* per pot						
No fertilizer	21.7	18.6	3.1*	22.1	23.0	−0.9
90 kg N ha^{-1}	20.4	11.3	9.1***	23.9	26.3	−2.4
40 kg P ha^{-1}	23.3	10.3	13.0***	23.5	26.2	−2.7
90 kg NPK ha^{-1}	22.7	12.8	9.9***	24.3	25.2	−0.9
LSD	3.79	3.79		3.79	3.79	
Aboveground maize biomass (g per pot)						
No fertilizer	3.9	5.2	−1.3*	4.7	7.1	−2.4*
90 kg N ha^{-1}	7.8	20.0	−12.2***	5.1	10.1	−5.0***
40 kg P ha^{-1}	5.4	19.8	−14.4***	3.2	9.7	−6.5***
90 kg NPK ha^{-1}	7.0	17.6	−10.6***	4.5	8.5	−4.0***
LSD	1.83	1.83		1.83	1.83	

* Significant at 5% probability.
*** Significant at 0.1% probability.

than recorded after a soybean crop that did not receive the herbicide application (Table 3). This increase in *S. hermonthica* emergence after a soybean crop was accompanied by a 27% reduction ($P \leq 0.001$) in maize biomass. Conversely, in pasteurized soil, there was no significant difference in number of emerged *S. hermonthica* plants or maize biomass between the imazaquin and no herbicide application treatments to a preceding soybean crop (Table 3). There was only a slight decrease in the number of emerged *S. hermonthica* in maize grown in natural soil with nicosulfuron applied to a preceding maize crop (Table 3). In pasteurized soil, there was no significant difference in the number of emerged *S. hermonthica* plants in maize or in the aboveground biomass of maize with or without nicosulfuron application to a preceding maize crop.

Similarly, in natural soil with no herbicide applied to the preceding crop, application of N, P, or NPK to a preceding soybean crop reduced ($P = 0.05$) the number of emerged *S. hermonthica* plants and increased ($P \leq 0.001$) maize biomass compared with a preceding soybean crop without fertilizer application (Table 4). In pasteurized soil, there was no reduction in *S. hermonthica* emergence following N, P, or NPK application to a preceding soybean crop (Table 4). In natural soil where nicosulfuron or imazaquin was applied to a preceding crop, application of N, P, or NPK

had a similar effect as to the soil being pasteurized (Tables 3 and 4).

4. Discussion

Reduction of *S. hermonthica* parasitism in maize occurred in the first cropping cycle of this study when nicosulfuron was applied to the maize crop (Table 1). This supports earlier findings (Berner et al., 1997a) on the efficacy of nicosulfuron to reduce *S. hermonthica* parasitism in both pot and field experiments. While the direct effect of N fertility on maize growth and biomass accumulation is well known, reduction in the number of emerged *S. hermonthica* as a result of application of N fertilizer has also been reported previously (e.g. Farina et al., 1985; Kim and Winslow, 1992; Ahonsi et al., 2002a). By contrast, several other workers have reported either no effect or stimulatory effect of N fertility on *S. hermonthica* emergence (e.g. Gworgwor, 1993; Oswald et al., 1997). Ahonsi et al. (2002a) showed that observed effect of increase in soil N on *S. hermonthica* parasitism in maize is dependent on the existence of natural soil suppressiveness. When natural soil suppressiveness to *S. hermonthica* is present, increase in soil N leads to significant reductions in the number of *S. hermonthica* plants infecting maize. However, when the soil is not naturally

suppressive, the immediate effect of increasing soil N would be a concomitant increase in the number of *S. hermonthica* plants infecting maize. The effect of balanced NPK application on *S. hermonthica* emergence is less well understood compared with application of N alone. Mills and Senghore (1991) found that application of balanced NPK in cereals was beneficial and more cost effective than application of N only as urea. Phosphorous, which is required less by maize than by legumes, not only had no effect on the number of emerged *S. hermonthica* plants but also did not significantly affect maize dry matter accumulation in the first cropping cycle. This is consistent with previous reports (e.g. Farina et al., 1985; Bebawi, 1987; Gworgwor, 1993) that P has no effect on *Striga* spp. emergence in cereals.

The soybean crop may have contributed to soil N through biological N_2-fixation, some of which was available to the subsequent maize crop (Peoples et al., 1995; Carsky et al., 1997). The increase in N availability may have also resulted from soybean absorbing less soil nitrate ('nitrate-sparing' effect) than maize, leaving more for the subsequent maize (Peoples et al., 1995; Carsky et al., 1997). Crop rotation with legumes is also reported to increase availability of nutrients other than N through increased soil microbial activity (Kucey et al., 1988; Ladha et al., 1989; Wani et al., 1995). This complex biological interaction presumably led to the increase in soil suppressiveness to *S. hermonthica* in the bioassay maize crop. Because parasite seeds were added to soils after the first crop, the reduction in number of *S. hermonthica* emerging in this study was not directly related to the ability of some soybean varieties to deplete *S. hermonthica* seed reserves in soil through suicidal germination (Berner et al., 1996; Carsky et al., 2000; Dashiell et al., 2000; Oswald and Ransom, 2001). What was measured was microbial induced suppressiveness, enhanced by increased soil nitrogen resulting from legume cropping (Ahonsi et al., 2002a); an effect that normally coexists with suicidal germination of *Striga* seeds by the legume crop in field studies (Berner et al., 1996; Oswald and Ransom, 2001). The results indicate that breeding legumes for rotation with cereals to control *S. hermonthica* should focus not only on increasing the *Striga* spp. seed germination ability of legume cultivars, but also on improving biological N_2-fixation.

The toxicity of ALS inhibiting herbicides, even at very low rates, to soil-borne organisms has been reported widely (e.g. Ray, 1982; O'Keefe et al., 1987, 1988; LaRossa and Van Dyk, 1988, 1989; Burnet and Hodgson, 1991; Dumontet et al., 1993; Forlani et al., 1995; Whitcomb, 1999). O'Keefe et al. (1987, 1988) reported that inhibitors of ALS adversely affect prokaryotic microbes, while Martensson and Nilsson (1989) reported that one of the sulfonylureas, chlorsulfuron inhibited the normal development of nitrogen-fixing *Rhizobium* nodules on alfalfa and red clover. Mallik and Tsefai (1985) and Kucey et al. (1988) had earlier reported reductions in biological N_2-fixation due to herbicide applications through their harmful effects on *Bradyrhizobium japonicum* strains in soils. Specifically, the use of imazaquin has been patented as a method to reduce soil-borne fungi (Berner et al., 1992).

Also, the persistent nature and non-target effects of ALS-inhibiting herbicides are well reviewed and documented by Whitcomb (1999). Several authors have reported soil persistence and ecotoxicity of imidazolinones and imazaquin (Mills and Witt, 1989; Mangels, 1991; Loux and Reese, 1993; Evbuomwan et al., 1993; Milanova and Grigorov, 1996; Baughman et al., 1997). Indeed, LaRossa and Van Dyk (1989) have concluded that the inhibition of ALS results in a cascade ending in metabolic poisoning, while Burnet and Hodgson (1991) explained that the application of ALS-inhibiting herbicides significantly affects the ecological balance of microorganisms in the soil. Results of the present study indicate that ALS-inhibiting herbicides, particularly imazaquin used in the preceding soybean crop, adversely affected soil micro-organisms and greatly reduced biotic soil suppressiveness to *S. hermonthica*. Follow-up experiments should be conducted to see if this effect is as pronounced under field conditions, although the literature suggests that it may be. If so, the short-term benefits derived from use of ALS-inhibiting herbicides may be outweighed by long-term detrimental effects to naturally occurring soil suppressiveness to *S. hermonthica*.

Residual effects of N, P, and NPK on *S. hermonthica* parasitism on the bioassay maize crop were observed only in natural soil without herbicide and not in pasteurized soil or in natural soil where ALS-inhibiting herbicides were applied. This indicated that positive

effects of fertilization on reducing *S. hermonthica* parasitism were only evident when soil-suppressiveness was not altered. Since P did not directly affect *S. hermonthica* parasitism in maize (Table 1), reduced *S. hermonthica* emergence in the bioassay maize crop planted in natural soil after a soybean crop that received P (Table 4) could have resulted from increased N_2-fixation (Giller and Cadisch, 1995). For N, and NPK applied to preceding crop, in addition to the direct effect of residual soil N (Peoples et al., 1995), N_2-fixation by the preceding soybean crop probably increased the level of N available in soil for the subsequent maize crop. It is therefore not surprising that reduction in *S. hermonthica* parasitism from previous application of N, P, and NPK was evident on maize planted in natural soil preceded by a soybean crop but not a maize crop (Table 4). While rotation of cereals with N-fixing legumes is a central management strategy for reducing the problem of *S. hermonthica* in Africa, good management of the legume crop preceding cereals (O'Hara et al., 1988; Giller and Cadisch, 1995), could also be an important way of improving natural soil suppressiveness to *S. hermonthica*. This is indicated by the high reduction of *S. hermonthica* parasitism resulting from P application to a preceding soybean crop in this study (Table 4).

5. Conclusions

From this study, it may be concluded that soil suppressiveness to *S. hermonthica* is microbial in nature, and an important factor that needs consideration in integrated *S. hermonthica* management (ISM) because soil suppressiveness is influenced by land-based *Striga* management practices. Practicing legume rotation with cereals and good management of the legume crop, through fertilizer application, appears to enhance the level of biotic soil suppressiveness to *S. hermonthica*. The use of chemical herbicides such as ALS-inhibiting herbicides may be useful in the control of *S. hermonthica* in the short-term, but these herbicides may pose a long-term risk to naturally existing biotic soil suppressiveness to the parasite. The net result could be even more serious *Striga* problems (e.g. herbicide-resistant biotypes developed, while efficacies of natural soil suppressiveness dependent *Striga* management practices are diminished) and less

food in Africa. Careful evaluation of the advantages and risks of the use of ALS-inhibiting herbicides as a primary control strategy for *S. hermonthica* is warranted.

Acknowledgements

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